Report

Current Biology

Parallel Emergence of True Handedness in the Evolution of Marsupials and Placentals

Highlights

- Bipedal macropod marsupials display population-level left-forelimb preference
- Lateralization in bipedal marsupials is consistent across multiple behaviors
- Bipedal marsupials show stronger manual lateralization than quadrupeds
- Species differences in lateralization are not explained by phylogenetic relations

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In Brief

Strongly pronounced handedness is traditionally considered to be a distinctive human trait. Giljov et al. show forelimb preferences in kangaroos, comparable in strength with human handedness, but oppositely directed. The contrast in manual lateralization between bipedal and quadrupedal marsupials emphasizes the link between posture and handedness.

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Parallel Emergence of True Handedness in the Evolution of Marsupials and Placentals

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SUMMARY

Recent studies have demonstrated a close resemblance between some handedness patterns in great apes and humans [1–3]. Despite this, comparative systematic investigations of manual lateralization in non-primate mammals are very limited [4, 5]. Among mammals, robust population-level handedness is still considered to be a distinctive human trait [6, 7]. Nevertheless, the comprehensive understanding of handedness evolution in mammals cannot be achieved without considering the other large mammalian lineage, marsupials. This study was designed to investigate manual lateralization in non-primate mammals using the methodological approach applied in primate studies. Here we show that bipedal macropod marsupials display left-forelimb preference at the population level in a variety of behaviors in the wild. In eastern gray and red kangaroos, we found consistent manual lateralization across multiple behaviors. This result challenges the notion that in mammals the emergence of strong "true" handedness is a unique feature of primate evolution. The robust lateralization in bipedal marsupials stands in contrast to the relatively weak forelimb preferences in marsupial quadrupeds, emphasizing the role of postural characteristics in the evolution of manual lateralization as previously suggested for primates [8–10]. Comparison of forelimb preferences in seven marsupial species leads to the conclusion that the interspecies differences in manual lateralization cannot be explained by phylogenetic relations, but rather are shaped by ecological adaptations. Species' postural characteristics, especially bipedality, are argued to be instrumental in the origin of handedness in mammals.

RESULTS

Distribution of Individual Preferences

Here we examined forelimb preferences in a variety of natural, not artificially evoked, behaviors in four species of macropod marsupials (Figure 1). The distributions of individual forelimb preferences are shown in Tables S1–S4.

In Goodfellow's tree-kangaroo, *Dendrolagus goodfellowi*, there was a similar distribution of preferences in both feeding from the bipedal position and feeding from the quadrupedal position. No significant difference was found between the number of lateralized and non-lateralized tree-kangaroos (binomial $z = 1.34$, $p = 0.180$) or between the number of left-handed and right-handed individuals ($z = -0.32$, $p = 0.754$). When supporting the body in the tripedal stance, no significant difference was found between the number of lateralized and non-lateralized tree-kangaroos (binomial $z = 1.34$, $p = 0.180$) or between the number of left-handed and right-handed individuals ($z = -0.95$, $p = 0.344$). For autogrooming there was no significant difference between the number of lateralized and non-lateralized individuals ($z = 1.34$, $p = 0.180$) or between the number of left- and right-handed individuals ($z = -0.32$, $p = 0.754$).

In the red-necked (Bennett's) wallaby, *Macropus* (*Notamacropus*) *rufogriseus*, significantly more individuals were lateralized than non-lateralized in feeding from the bipedal position (binomial $z = 2.91$, $p = 0.003$). Among lateralized wallabies, the majority preferred to use the left forelimb ($z = 2.91$, $p = 0.002$). In feeding from the quadrupedal position, the majority of individuals were lateralized (binomial $z = 2.43$, $p = 0.013$); however, there was no significant difference between the number of left- and right-handed individuals ($z = 1.34$, $p = 0.180$). When supporting the body in the tripedal stance, the majority of individuals were lateralized (binomial $z = 2.12$, $p = 0.031$) and there were significantly more right- than left-handed wallabies ($z = -2.94$, $p = 0.002$). For autogrooming, significantly more wallabies were lateralized than non-lateralized (binomial $z = 2.94$, $p = 0.002$), and all of the lateralized individuals showed preference for the left forelimb ($z = 3.33$, $p < 0.001$). Separately, we considered bimanual feeding, when individuals differentially used two forelimbs to feed on trees and shrubs. In the majority of observations (only single observations per individual were included in the analysis), red-necked wallabies used the left forelimb for directing stems and leaves to the mouth and the right forelimb for supporting branches (35 out of 42 observations; binomial $z = 4.17$, $p < 0.001$).

In the eastern gray kangaroo, *Macropus* (*Macropus*) *giganteus*, significantly more individuals were lateralized than non-lateralized in feeding from the bipedal position (binomial $z = 2.75$, $p = 0.004$). There were significantly more left- than right-handed kangaroos ($z = 3.25$, $p < 0.001$). When feeding from the quadrupedal position, a significant majority of individuals showed

Figure 1. Forelimb Use in Wild Red-Necked Wallabies, *Macropus* (*Notamacropus*) *rufogriseus*

Feeding from the bipedal position (A), feeding from the quadrupedal position (B), supporting the body in the tripedal stance (C), and bimanual feeding on trees and shrubs (D). The forelimb preferences were assessed separately in each type of behavior for each individually identified animal. See also Figure S1.

individual forelimb preferences (binomial $z = 2.35$, $p = 0.017$). There were more left- than right-handed kangaroos ($z = 2.43$, $p = 0.013$). When supporting the body in the tripedal stance, significantly more individuals were lateralized than non-lateralized (binomial $z = 2.40$, $p = 0.015$), and the majority of lateralized individuals were left-handed ($z = 2.29$, $p = 0.019$). Significantly more eastern gray kangaroos were lateralized than non-lateralized in autogrooming (binomial $z = 2.97$, $p = 0.002$). Significantly more individuals showed left- rather than right-forelimb preference ($z = 3.34$, $p < 0.001$).

In the red kangaroo, *Macropus* (*Osphranter*) *rufus*, the significant majority of individuals were lateralized in feeding from the bipedal position ($z = 3.49$, $p < 0.001$), and there were significantly more left- than right-handed individuals ($z = 3.67$, $p < 0.001$). For feeding from the quadrupedal position, significantly more red kangaroos were lateralized than non-lateralized (binomial $z = 3.59$, $p < 0.001$), and the majority of lateralized individuals showed left-forelimb preference ($z = 3.06$, $p = 0.002$). When supporting the body at the tripedal stance, there was a significant prevalence of lateralized individuals (binomial $z = 2.75$, $p = 0.004$), and the majority were left-handed ($z = 2.41$, $p = 0.013$). Similar to other types of behavior, for autogrooming, significantly more red kangaroos were lateralized than non-lateralized (binomial $z = 3.80$, $p < 0.001$). There were significantly more left- than right-handed individuals ($z = 3.67$, $p < 0.001$).

Direction and Consistency of Lateralization

In Goodfellow's tree-kangaroo, no significant population-level preference was shown in any type of behavior ($p > 0.05$; Table S5). Analysis failed to reveal any significant influence of the type of behavior on manual lateralization (Friedman's test: $\chi^2_{(3)} = 2.31$, $p = 0.510$).

In red-necked wallabies, the expression of population-level lateralization differed between the types of behavior (see Table S5). In feeding from the bipedal position, individuals were significantly more left-handed compared to feeding from the quadrupedal position (Wilcoxon matched-pairs signed-rank test: $Z = -59$, $p = 0.040$; $n_1 = n_2 = 13$) and supporting the body in the tripedal stance ($Z = -108$, $p < 0.001$; $n_1 = n_2 = 15$). Red-necked wallabies were significantly more left-handed in autogrooming than in both feeding from the quadrupedal position ($Z = 11$, $p = 0.007$; $n_1 = n_2 = 11$) and supporting the body in the tripedal stance ($Z = 10$, $p = 0.002$; $n_1 = n_2 = 10$). When feeding from the quadrupedal position, wallabies were significantly more left-handed than when supporting the body in the tripedal stance ($Z = -56$, $p = 0.027$; $n_1 = n_2 = 12$). No difference was found between feeding from the bipedal position and autogrooming ($Z = 48$, $p = 0.064$; $n_1 = n_2 = 13$).

Eastern gray and red kangaroos both showed a population-level preference for the left forelimb in all types of behavior ($p < 0.05$; Table S5). Analysis failed to reveal any significant influence of behavioral type on preferences in forelimb use in red kangaroos ($p > 0.05$, Wilcoxon matched-pairs signed-rank test). In eastern gray kangaroos, the type of behavior influenced manual lateralization. When feeding from the bipedal position, individuals were significantly more left-handed than when feeding from the quadrupedal position ($Z = -41$, $p = 0.037$; $n_1 = n_2 = 10$) or when supporting the body at the tripedal stance ($Z = -62$, $p = 0.012$; $n_1 = n_2 = 12$). Individuals were also significantly more left-handed in autogrooming than in both feeding from the quadrupedal position ($Z = 118$, $p = 0.012$; $n_1 = n_2 = 19$) and supporting the body at the tripedal stance ($Z = 86$, $p = 0.025$; $n_1 = n_2 = 16$). No significant difference was found between feeding from the bipedal position and autogrooming or between feeding from the quadrupedal position and supporting the body at the tripedal stance ($p > 0.05$).

Subjects' sex was shown to have no significant influence on manual lateralization in all four species studied ($p > 0.05$; Table S5).

Interspecies Comparison

The interspecies comparison includes four species of Macropodidae family investigated in the present study and three marsupial species studied previously: gray short-tailed opossums (Didelphidae [11]), sugar gliders (Petauridae [11]), and brush-tailed bettongs (Potoroidae [12]). In each species, manual

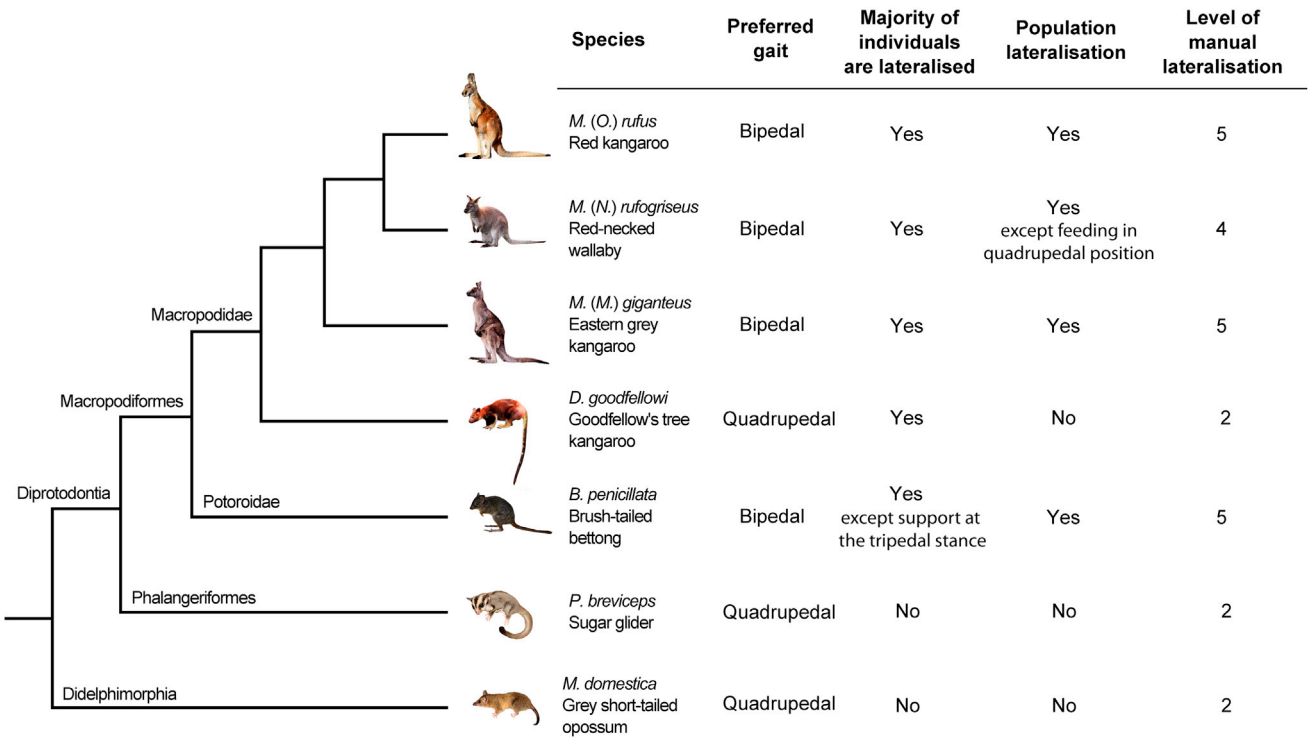

Figure 2. Lateralization of Forelimb Use in Marsupials

Simplified cladogram of the extant Marsupialia (based on [13, 14]) including only the species studied in terms of manual lateralization. Whether or not the majority of individuals are lateralized and population lateralization is found in all four studied types of unimanual behavior is given for each species (see Table S5). The level of manual lateralization was determined using the criteria described in the Supplemental Experimental Procedures. Gray short-tailed opossums, *Monodelphis domestica*, and sugar gliders, *Petaurus breviceps*, are both obligatory quadrupeds [15, 16]. Goodfellow's tree-kangaroos, *Dendrolagus goodfellowi*, are able to move bipedally but mainly use the quadrupedal gait and have lost many adaptations to terrestrial bipedal locomotion due to their arboreal lifestyle [17, 18]. Adaptations to bipedalism in the eastern gray kangaroo, *Macropus* (*Macropus*) *giganteus*, and the red kangaroo, *Macropus* (*Osphranter*) *rufus*, are among the most pronounced in extant macropodids [17], whereas the brush-tailed bettong, *Bettongia penicillata*, is one of the most bipedal members of the Potoroidae family [19]. Red-necked wallabies, *Macropus* (*Notamacropus*) *rufogriseus*, can move on all four legs at slow speeds but use bipedal locomotion as a preferred gait [20, 21]. See also Figure S2.

lateralization was classified by considering forelimb preferences at both individual and population levels (see Tables S1–S5). For each species, the level of lateralization was determined on four types of unimanual behavior, in which individual- and population-level forelimb preferences were statistically tested. The comparative results on all species are presented in Figure 2. The analysis failed to detect a phylogenetic signal in the distribution of levels of lateralization. The observed distribution of levels of lateralization (number of steps = 5) fell within the 95% confidence intervals (CIs) of the randomized distribution (mean number of steps = 5.07, lower 95% confidence interval = 0.01 [$\leq$2 steps], upper 95% confidence interval = 0.00 [>6 steps]). However, more marsupial species should be studied to confirm this result.

The interspecies differences were examined using a meta-analytic approach. The subgroup analysis with each species as a subgroup showed that bipedal species are significantly lateralized, whereas species using quadrupedal locomotion as a preferred gait are not, as indicated in the forest plot (Figure S2). The subgroup analysis with bipedal and quadrupedal species as two subgroups revealed that species' postural characteristics significantly influenced the estimate. In the four bipedal species, the pooled odds ratio was 2.35 (95% CI: 1.97, 2.77; z = 10.24, $p < 0.001$), whereas the odds ratio was 1.03 (95% CI: 0.80, 1.34; z = 0.25, p = 0.803) for the three quadrupedal species. The non-overlap of the confidence intervals indicates a statistical significance between bipedal and quadrupedal species. Random-effect meta-regression analysis revealed a significant difference between bipedal and quadrupedal species (regression coefficient = −0.83, $p < 0.001$). Random-effect meta-regression analysis also demonstrated the absence of difference ($p > 0.270$) between the types of behavior in all but one species. In red-necked wallabies, *M*. (*N*.) *rufogriseus*, lateralization in supporting the body in the tripedal stance differed significantly from other types of behavior and was opposite to them in direction (regression coefficient = −1.66, $p < 0.001$).

DISCUSSION

Across the marsupials studied here, lateralization of forelimb use is especially pronounced in eastern gray and red kangaroos. Eastern gray and red kangaroos showed robust and consistent patterns of manual lateralization uncommon even for intensively studied placental mammals [4]. For example, in non-human primate species, lateralization of forelimb use at the population level is only found in specific tasks, such as bimanual feeding,

Figure 3. Population-Level Lateralization of Unimanual Feeding in Marsupials

Mean handedness index scores for feeding from the bipedal body position are presented for Goodfellow's tree-kangaroo, *Dendrolagus goodfellowi* (n = 14); the eastern gray kangaroo, *Macropus* (*Macropus*) *giganteus* (n = 19); the red-necked wallaby, *Macropus* (*Notamacropus*) *rufogriseus* (n = 20); the red kangaroo, *Macropus* (*Osphranter*) *rufus* (n = 21) (the present study); and the brush-tailed bettong, *Bettongia penicillata* (n = 15) [12]. Mean handedness index scores for feeding from the quadrupedal body position (feeding from the bipedal position is not typical behavior) are presented for gray short-tailed opossums, *Monodelphis domestica* (n = 26), and sugar gliders, *Petaurus breviceps* (n = 23) [11]. Asterisks indicate the significant lateralization in forelimb use at the population level (one-sample Wilcoxon signed-rank test, two-sided). **$p < 0.01$, ***$p < 0.001$; NS, non-significant. Positive values indicate left-forelimb bias; negative values indicate right-forelimb bias. Error bars indicate the SEM. See also Tables S1–S4.

and is not consistently expressed across a number of different behaviors ([22–24], but see [25] for one exception). Consistent one-hand preference at the population level across a wide range of behaviors (so-called "true" handedness [26]) is considered to be a characteristic of humans [8, 27, 28]. The results of the present study and mounting evidence of the striking similarities between human handedness and the lateralization of forelimb use in other animals [3, 29–31] challenge the traditional belief in the evolutionary uniqueness of human handedness. Findings in vertebrates besides mammals [4, 32] and in invertebrates (see [33, 34] for complementary reviews) further suggest that strongly lateralized limb use is more widespread than previously thought [5].

We have used the comparative approach to summarize the results on lateralization of forelimb use in the marsupial mammals studied to date. The interspecies differences in the expression of manual lateralization found in marsupials (Figure 2) do not seem to be associated with phylogenetic relations. Indeed, the members of different families—gray short-tailed opossums, *Monodelphis domestica* (Didelphidae), sugar gliders, *Petaurus breviceps* (Petauridae), and Goodfellow's tree-kangaroos (Macropodidae)—all have the same level of lateralization, whereas the members of the same family (Macropodidae)—Goodfellow's tree-kangaroos, red-necked wallabies, and eastern gray and red kangaroos—display different levels of lateralization. In a similar way, primate handedness patterns appear to not be related to the phylogenetic affinities of the species [24, 35]. For example, it has been argued that the interspecies differences in the forelimb preferences of great apes are related to ecological adaptations rather than to phylogeny [1, 24].

The studied marsupial species with quadrupedal locomotion as a preferred gait show low levels of lateralization (Figure 2). There is strong evidence that tree-kangaroos have evolved from bipedal terrestrial macropods and are secondarily adapted to an arboreal lifestyle and quadrupedal locomotion [18]. Thus, both primary (e.g., the gray short-tailed opossum) and secondary (Goodfellow's tree-kangaroo) marsupial quadrupeds do not display pronounced handedness, providing further evidence in favor of the hypothesis that quadrupedality hinders the expression of population forelimb preferences [12, 36]. Marsupials using bipedal locomotion as a preferred gait tend to show higher levels of lateralization compared to species which are mainly quadrupedal (Figure 2). This contrast between bipedal and quadrupedal species is conspicuous (Figure 3) when considering the expression of population-level forelimb preferences for feeding in all seven studied marsupials. In primates, bipedality has also been shown to be associated with enhanced manual lateralization (e.g., [8, 10, 37, 38]). Bipedalism, along with other factors [3, 24], has been suggested as a catalyst for the emergence of robust handedness in humans [8, 39]. Our findings on marsupials further emphasize the role of bipedality in the evolution of manual lateralization. Species postural characteristics are likely to be an important contributor to variations in handedness, not only in primates but for mammals in general. In both groups—primates and marsupials—the most pronounced examples of handedness have been found in strongly bipedal species as opposed to quadrupeds (Figure 4). Only those species with bipedal locomotion display consistent manual lateralization across multiple behaviors in both groups. Similar correlations (apparently non-causal) between bipedal posture and handedness have been shown by distinct groups of mammals, pointing to a universal physiological principle for how postural adaptations impact on handedness.

According to the "postural origins" theory [41, 42], an arboreal lifestyle favored the emergence of functional specializations of the left and right hands for feeding and postural support in primates. We failed to find evidence of forelimb specializations in the most arboreal species studied—sugar gliders [11] and Goodfellow's tree-kangaroos (the present study). A division of functions between the forelimbs was found, however, in terrestrial species. Red-necked wallabies preferred the left forelimb for autogrooming and feeding from a bipedal position, but used the right forelimb preferentially for unimanual body support in the tripedal stance (also initiated from the bipedal position). We

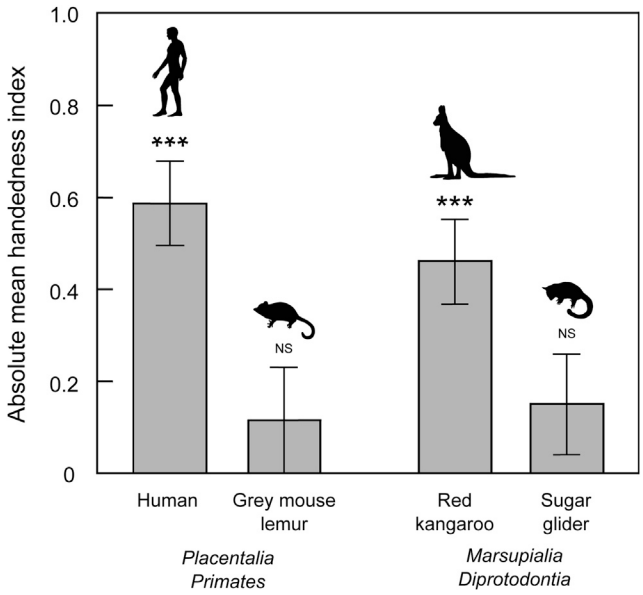

Figure 4. Lateralization in Unimanual Feeding of Bipedal versus Quadrupedal Primates and Marsupials

Highly bipedal versus fully quadrupedal members of the placental order Primates (humans and gray mouse lemurs [*Microcebus murinus*], respectively) and the marsupial order Diprotontia (red kangaroos [*Macropus* (*Osphranter*) *rufus*] and sugar gliders [*Petaurus breviceps*], respectively) are presented. Only the species strikingly different in the degree of bipedality are included. The figure illustrates the general tendency of habitually bipedal species to show more pronounced population lateralization in unimanual forelimb use as compared with the mostly quadrupedal species. For each species, the absolute value of mean handedness index score ± SEM is shown to characterize the degree of manual lateralization irrespective to the direction. The population lateralization in each species was examined using directional handedness index scores for unimanual food reaching performed from the quadrupedal body position (humans: n = 32, one-sample t test on data from [8]; gray mouse lemurs: n = 44, one-sample Wilcoxon signed-rank test on data from [40]; red kangaroos: n = 28, one-sample Wilcoxon signed-rank test [present study]; sugar gliders: n = 23, one-sample Wilcoxon signed-rank test on data from [11]). All tests were two sided. Asterisks indicate the significant lateralization in forelimb use at the population level. ***p < 0.001; NS, non-significant.

further show that red-necked wallabies prefer the left forelimb for directing stems and leaves to the mouth and the right forelimb for supporting the branches when feeding bimanually on trees and shrubs. The division of labor between the left and right forelimbs in both unimanual and bimanual behaviors seems to be determined by the nature of the action. The left forelimb is preferred by red-necked wallabies in tasks that involve fine manipulation, whereas the right forelimb is preferentially used in static tasks that require physical strength. The absence of specializations in forelimb functions in species closely related to the red-necked wallaby—eastern gray and red kangaroos may be explained by interspecies differences in feeding ecology. In contrast to the studied kangaroo species, which are both grazers, the diet of red-necked wallabies includes a high proportion of trees and shrubs [43]. Browsing may require specific motor demands, such as the simultaneous use of two forelimbs for manipulations (Figure 1D). The emergence of differential roles for left and right forelimbs may be associated with the need to perform distinct manual tasks during bimanual feeding. Thus, we hypothesize that the specializations of forelimb functions in red-necked wallabies have been shaped under the pressure of ecological factors. This interpretation is consistent with the general evidence for high evolutionary plasticity in motor and sensory lateralization (e.g., [35, 44–47]).

Population-level forelimb preferences are widely considered to be underpinned by hemispheric asymmetry [48]. The neural basis of manual lateralization found in bipedal marsupials is unknown. Correlation between the structural asymmetry of the motor cortex and lateralized use of the forelimbs has been shown in placental mammals [49]. To our knowledge, asymmetry of the motor cortex in marsupials has not been reported to date. Existing data indicate that there may be some substantial differences between placentals and marsupials in the neuroanatomical mechanisms determining manual lateralization. In contrast to placentals, brush-tailed possums (*Trichosurus vulpecula*) do not shift their manual preferences, despite having large cortical lesions in the brain hemispheres that are contralateral to their preferred forelimb [50]. Thus, the neurobiology of manual lateralization in marsupials is an important subject for future research.

Ethical Note

Observations of macropod behavior in the wild were conducted with the approval of the University of Tasmania Animal Ethics Committee (ethics no. A12129), the Department of Primary Industries, Parks, Water and Environment, Tasmania (permit no. FA12070), and the NSW National Parks & Wildlife Service (scientific license no. 101054).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures, two figures, and five tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.05.043.

AUTHOR CONTRIBUTIONS

A.G. and K.K. designed the study, collected the data, performed the data analysis, and conceptualized and wrote the paper. J.I. helped to collect the data, and conceptualized and edited the paper. Y.M. designed the study, collected the data, provided the grant support, and conceptualized and wrote the paper.

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